The intricate *Pinguicula crystallina/hirtiflora*-complex

Andreas Fleischmann • Botanische Staatssammlung München • Menzinger Strasse 67 • D-80638 Munich • Germany • fleischmann@lrz.uni-muenchen.de

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The *Pinguicula crystallina/hirtiflora*-species-aggregate (*Pinguicula* section *Cardiophyllum*, which will be further simply called the "*P. crystallina*-complex" here) comprises rosetted perennial temperate butterworts of homophyllous growth type (the latter means that carnivorous leaves are produced throughout the year, no hibernacula or non-carnivorous winter leaves are present, and the plants hibernate with open leaf rosettes) that are distributed in the Mediterranean (southern Italy, the Balkans, and Greece) and Asia Minor (Cyprus and Turkey).

Taxonomic history and difficulties of this intricate group of *Pinguicula* have been dealt in detail by Ernst (1961), Casper (1962, 1966, 1970, 2004, 2006), Peruzzi (2006), and Shuka *et al.* (2007), yet still many questions remained regarding species concepts and circumscriptions. The species-complex is reviewed here, based on newly available data on distribution, morphological plasticity, and chromosome numbers, based on own field and herbarium studies, as well as on data gained from plants in cultivation.

Four morphologically quite distinct taxa can be distinguished in this natural affinity, based on corolla shape, and leaf shape and size. Biogeography, size and ultrastructure of the seeds, as well as cytology (diploids and tetraploids, based on a common chromosome base number of $x = 14$; Casper & Stimper 2009) generally support these four lineages. In accordance, three of the four taxa of this complex are treated here as separate species, one on variety rank: *Pinguicula crystallina*, *P. hirtiflora* var. *hirtiflora*, *P. hirtiflora* var. *louisii*, and *P. megaspilaea*. A comparative treatment of these four taxa is given below.

Material and Methods

Information about distribution, habitats, as well as morphological data is based on examination of herbarium specimens and digitized images thereof (AIX, B, G, K, M, MARS, P, WU), on own observations of plants *in situ* and in cultivation, as well as extracted from literature (i.e. all sources listed under "References").

Identification key to the species of the *P. crystallina* -complex:

1. Lobes of corolla upper lip distinctly smaller (shorter and narrower) than those of the lower lip, spur 4-6(-8) mm long (1/3 of the corolla length) ... *P. crystallina*
- Lobes of corolla upper and lower lip (sub)equal in size, spur longer than 6 mm (usually 7-20 mm long, comprising more than half of the corolla length) ... 2
2. Lobes of the lower and upper corolla lip rounded, obtuse or slightly truncate; fully grown summer leaves usually with reflexed margins (the very margin only slightly enrolled); leaves of summer growth usually half-erect ... 3
- Lobes of the lower (and usually also upper) corolla lip notably truncate to emarginate; leaves with distinctly enrolled margins; leaves of summer growth usually prostrate on the ground ... *P. hirtiflora* var. *hirtiflora*
3. Leaves of summer growth 1-2 cm long (rarely up to 8 cm), oblong-elliptic to obovate; spur (8-)13-22 mm long, equaling to exceeding the length of the rest of the corolla ... *P. hirtiflora* var. *louisii*

- Leaves of summer growth 4-12 cm long, very narrowly (ob)lanceolate to linear, their very margins reflexed; spur 6-11 mm long, notably shorter than the rest of the corolla (tube + spread lips) ... *P. megaspilaea*

Pinguicula crystallina Sm.

Leaves 15-25(-40) mm long, 10-25 mm wide, broadly elliptic to oblong, with distinctly enrolled margins and emarginate or obtuse apex; "winter leaves" only slightly smaller; leaves yellowish green or (rarely) tinged purple-reddish. *Scapes* 30-60(-100) mm long, densely glandular. *Calyx* bilabiate, upper lip trilobate (sepals free almost to the base), lower lip bilobate, lobes fused for half or more of their length, with obtuse apices. *Corolla* 8-15(-21) mm long (including spur), bilabiate, upper and lower lip forming an angle of ca. 90° or more, corolla white, each corolla lobe with violet-blue tip (sometimes lobes entirely white), corolla throat and spur yellowish-green, throat with few reddish-brown stripes; upper lip two-lobed, lobes widely divergent, with obtuse apex; lower trilobed, lobes spreading or slightly overlapping, each with obtuse to slightly truncate apex; spur narrowly cylindrical, (3-)4-6(-8) mm long, slightly curved downwards or straight. *Seeds* 0.7-0.85 mm long, cylindrical to ellipsoidal, testa reticulate (Mikeladse 1996).

Chromosome number: $2n = 28$ (Mikeladse 1996; Mikeladse & Casper 1997; Casper & Stimper 2004, 2006, 2009; Casper *et al.* 2007, all for material from Cyprus).

Etymology: The epithet *crystallina* (Lat. "of crystal") was chosen by the species' author, James Edward Smith, because of "the clear drops on its leaves glittering like diamonds in the sunshine" (Holmboe 1914).

Distribution: Cyprus, Turkey (Fig. 1). On Cyprus limited to the central part of the Troodos Mountains of Western Cyprus (seven populations are known from the Troodos Forest National Park; Georghiou *et al.* 2007), however an outlying lowland population has recently been discovered in

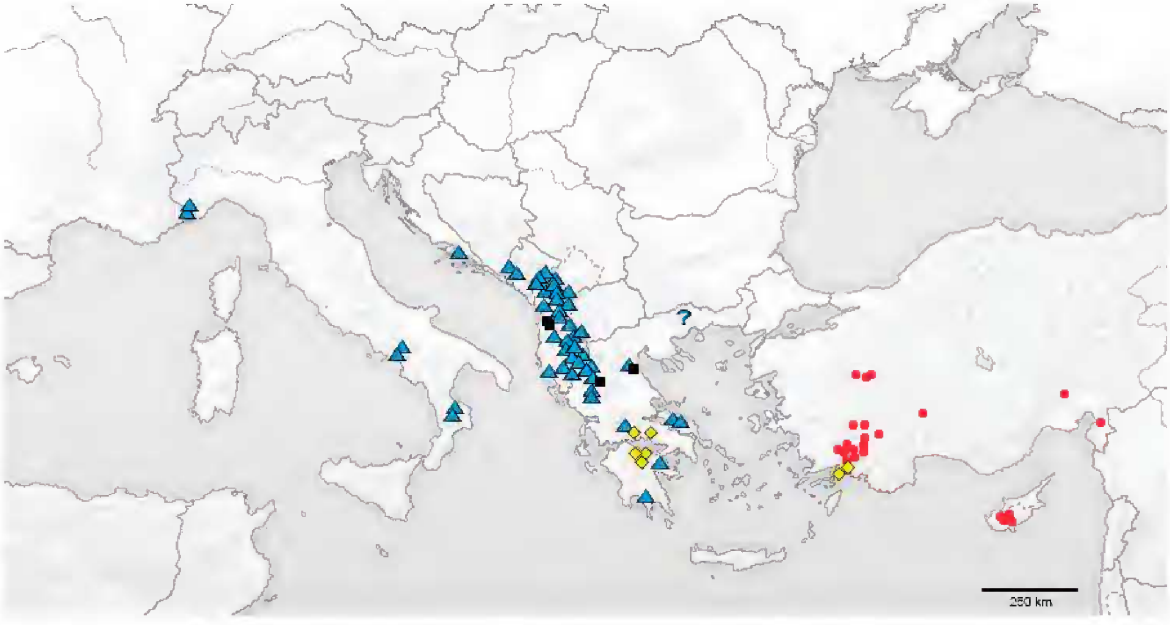

Figure 1: The distribution of the *P. crystallina*-complex in the Mediterranean and Asia Minor. *P. crystallina* (red dots), *P. hirtiflora* var. *hirtiflora* (blue triangles), *P. hirtiflora* var. *louisii* (black squares), and *P. megaspilaea* (yellow diamonds). The blue question mark refers to a doubtful literature record of *P. hirtiflora* from the Falakro Mountain of NE Greece.

the Lemesos Forest (Christodoulou 2006). In Turkey, the species occurs widespread, yet localized, in SW Anatolia (Mill 1978), but also in disjunct populations in S Anatolia (Adana and Hatay provinces; Yildirim *et al.* 2012), the latter in the south-east of the country close to the Syrian border (foothills of the Nur Dağlari Mountains; Adamec 1996, 1997; Adamec & Pasek 2000).

Habitat: On Cyprus at 800-1640(1900) m elevation in the Troodos Mountains (Casper 1970; Steiger 1998; Georghiou *et al.* 2007), but the outlying population in the Lemesos Forest at just 250 m altitude (Christodoulou 2006). In Turkey in montane regions (1000-1700 m; Casper 1970), but again as low as ca. 250 m in canyons of the foothills of the Nur Dağlari Mountains in SE Turkey (Adamec 1997). The species is confined to permanently wet habitats, where it grows as a lithophyte on wet rocks (Fig. 2), near springs, streams, and waterfalls, but also in peat soil in boggy seepage habitats. Usually found growing over serpentine rock (e.g. Cyprus, Sandras Mountains of Turkey), but also on limestone (e.g. mountains of Denizli province, Turkey), and in SE Turkey on basaltic rock associated with very alkaline water (Adamec 1996, 1997; Adamec & Pasek 2000). The high altitude populations of this species hibernate as open, carnivorous leaf rosettes covered by snow and ice.

Conservation status: Vulnerable on Cyprus (only eight populations are known from the island) and also vulnerable in Turkey, where the species is more widespread, but occurs in localized populations. Populations both on Cyprus and in Turkey are under potential threat by human influence on the hydrology (e.g. by spring capture or channeling), by road construction, but also by natural drought (Georghiou *et al.* 2007). Ironically, at least on paper, the species is strictly protected by the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, Appendix I).

Notes: Some of the previously used characters to distinguish *P. crystallina* from *P. hirtiflora* have proven unreliable, such as the shape and size of the leaves, the shape of the leaf tip (emarginate vs.

Figure 2: *Pinguicula crystallina* growing in the Troodos Mountains of Cyprus. Photos by Stewart McPherson.

Figure 3: *Pinguicula crystallina* in cultivation. Top: Plants from Mount Güneg, Denizli, Turkey (naturally growing on limestone). Bottom: Plants from Sandras Mountains, Muğla, Turkey (naturally growing on serpentine).

obtuse), or the indumentum inside the corolla throat (see Casper 1970), or the calyx shape, which is not different between the two species (Schindler 1908).

However the shape of the corolla, the length of the tubular part of the corolla, and the size of the spur allow readily to distinguish both taxa (Fig. 2, 3). Regarding the obvious close relationship of these two taxa, the question arose whether they should indeed be kept as distinct species, or if they are best considered two lineages of a single species. The latter has been put forward by Strid (1991), who treated the two species as geographically separated subspecies. Here, the "classical" approach (e.g. Schindler 1908; Ernst 1961; Casper 1966, 1970; Mikeladse & Casper 1997) to maintain both taxa as separate species is applied: the Anatolian-Cypriotic *P. crystallina* and the Italian-Balkan *P. hirtiflora* – there is no overlap evident in the range of the two species (see Fig. 1). Moreover, an artificially created hybrid between both species (using *P. hirtiflora* var. *hirtiflora* as the pollen donor and *P. crystallina* from Cyprus as the mother plant) proved to be male sterile (pollen is malformed, despite complementary chromosome numbers of both parent species), which indicates not only a geographical, but also a reproductive separation of both species. Interestingly, the hybrid resembles *P. hirtiflora* var. *hirtiflora* more in the vegetative parts, while the flowers show most characters of *P. crystallina*, such as a more tubular corolla with very short upper lip (Fig. 4).

Pinguicula megaspilaea Boiss. & Heldr. ex Boiss.

Synonyms: *P. hirtiflora* var. *megaspilaea* (Boiss. & Heldr. ex Boiss.) Schindler, *P. hirtiflora* subsp. *megaspilaea* (Boiss. & Heldr. ex Boiss.) Nyman, *P. hirtiflora* var. *gionae* Contandr. & Quezel, *P. habilii* Yıldırım, Şenol & Pirhan; as "*P. hirtiflora* var. *?*" in Casper *et al.* 2007

Leaves during anthesis (40-)70-120 mm long, 5-11 mm wide, very narrowly oblanceolate (lanceolate in the Turkish plants) to linear, usually with backwardly reflexed margins; "winter leaves" much shorter and slightly wider, 18-35 mm long, 11-16 mm wide, oblong to oblanceolate, with slightly enrolled margins; leaves yellowish green or tinged purple-reddish. *Scapes* 110-170 mm long, densely glandular. *Calyx* bilabiate, upper lip trilobate (sepals free almost to the base), lower

Figure 4: Artificially created hybrid between *P. hirtiflora* var. *hirtiflora* and *P. crystallina*, grown in the author's greenhouse. The plant does not produce viable pollen, but readily propagates by division of the mother rosette.

lobe entire (consisting of two fully fused sepals) with obtuse to truncate apex. *Corolla* 22-28 mm long (including spur), bilabiate, upper and lower lip spreading at ca. 180° (forming one line), corolla white, each corolla lobe with violet blue tip, corolla throat and spur yellowish-green, throat sometimes with few reddish-brown stripes; upper lip two-lobed, lobes widely divergent, with obtuse apex; lower lip trilobed, lobes slightly overlapping, each with obtuse to slightly truncate apex; spur narrowly cylindrical, 6-11 mm long, tapering towards acute apex. *Seeds* comparatively large and wide (compared to the other three members of the affinity), ca. 1 mm long, oblong to narrowly elliptical, testa reticulate (Yildirim *et al.* 2012).

Chromosome number: $2n = 56$ (Casper & Stimper 2006, 2009 and Casper *et al.* 2007, for material from Styx and Reka Gorge, Greece; haploid karyotype of Turkish plants $n = 28$, obtained from pollen mother cells from fixed flower buds of cultivated material, following the protocol from Casper & Stimper 2009). Contandriopoulos & Quezel (1974) counted $2n = 48$ from material from Styx, Greece, however this kayotype was put in question by Shuka *et al.* (2007) and Casper *et al.* (2007). This species has the double chromosome number of *P. hirtiflora*, hence could represent a tetraploid lineage.

Etymology: The epithet refers to the Megaspilaeon (or: Mega Spileon, Greek for "big cave") Monastery in the Chelmos Mountains, Peleponnese, Greece, where this species was first collected.

Distribution: Greece (Peloponnese: Chelmos Mountains, and Central Greece: Mt. Giona and Mt. Parnassus; Casper *et al.* 2007, from the latter localities reported as *P. hirtiflora* var. *gionae* and "*P. hirtiflora* var. *?*") and Turkey (known from a single population in Marmaris province (the type locality of *P. habilii*; Yildirim *et al.* 2012), as well as from a recently discovered second locality in Muğla province (pers. obs.)). This species shows an interesting disjunction, from the mountains of central Greece to the coastal region of SW Turkey (Fig. 1).

Habitat: Found growing lithophytically on serpentine rock at 80-200 m in SW Anatolia, Turkey (Yildirim *et al.* 2012; pers. obs.; Fig. 5). However, in Greece also on limestone rock and known from 650 m to up to 1930 m altitude (Contandriopoulos & Quezel 1974; Casper *et al.* 2007; J. Schlauer, pers. comms.). The populations in SW Anatolia are geographically (especially altitudinally) well-separated from the nearest known populations of *P. crystallina* (Yildirim *et al.* 2012; pers. obs.).

Conservation status: Considered critically endangered in Turkey due to human development (channeling, road construction; Yildirim *et al.* 2012). The few known populations in Greece are also best classified as endangered, as they are in potential threat by spring channeling (J. Schlauer, pers. comms.).

Notes: The plants described as *P. hirtiflora*. var. *gionae* from Greece by Contandriopoulos & Quezel (1974), agree morphologically (and cytologically: $2n = 56$, Casper & Stimper 2006) with *P. megaspilaea*, and are hence included in this species here.

Figure 5: *Pinguicula megaspilaea* growing on serpentine rock in Muğla province, Turkey. This is the second known location of this taxon from Turkey, where it has previously been described as *P. habilii* from Marmaris province.

This species differs much from the other members of the complex by producing long, upright leaves with reflexed margins during summer growth (Fig. 5; these "thread-like" leaves resemble those of the only distantly related *P. longifolia*). Elongate summer leaves are especially found in plants growing lithophytically on vertical rock – plants growing in boggy habitats (e.g. in the upper Styx valley) have leaves that are more similar to those of *P. hirtiflora* (J. Schlauer, pers. comms.). In terms of flower morphology, it is quite similar to *P. hirtiflora* (see Schindler 1908), except that *P. megaspilaea* usually has the tips of its corolla lobes entire and rounded (see Fig. 5), while these are usually emarginate in *P. hirtiflora*.

The "heterophyllous growth" which Yildirim *et al.* (2012) mention for their *P. habilii* does not correspond to the term "heterophyllous" as applied by Casper (1966) for his classification of *Pinguicula* growth types. The authors refer to the conspicuously longer, narrower carnivorous leaves produced during flowering time ("summer leaves"), compared to the much smaller, albeit still carnivorous "winter leaves" of this species – that means it is an anisophyllous species. A similar decrease of rosette diameter in autumn/winter can be observed in any of the three other members that belong to this affinity (*P.* section *Cardiophyllum*), too, as all of them produce (slightly to distinctly) smaller carnivorous leaves during this time. Nevertheless, all of them classify as the "temperate homophyllous growth type" as defined by Casper (1966), as continuous growth and production of carnivorous foliage occurs throughout the year.

Pinguicula hirtiflora var. *louisii* (Markgr.) A.Ernst

Synonyms: *P. louisii* Markgr., *P. hirtiflora* var. *decipiens* Bornm.

Leaves 10-20(-80) mm long, 6-10(-25) mm wide, oblong-elliptic to obovate, with just minutely enrolled margins, yellowish green or tinged purple-reddish (especially near the base). *Scapes* (30-) 40-150 mm long, sparsely glandular, glabrous towards the base. *Calyx* bilabiate, upper lip trilobate (sepals free almost to the base), lower lobe entire (consisting of two fully fused sepals), with obtuse or retuse, rarely emarginate, apex. *Corolla* 22-29 mm long (including the very long spur), bilabiate, upper and lower lip forming an angle of ca. 80°-110° (Casper 2004), corolla white, each corolla lobe with bright to pale violet-blue tip, corolla throat and spur yellowish-green, throat with few reddish-brown stripes; upper two-lobed, lobes divergent, or slightly overlapping, with rounded apex; lower lip trilobed, lobes oblong to almost orbicular, each lobe with rounded to only slightly

Figure 6: *Pinguicula hirtiflora* var. *louisii* growing at Mount Olympus, Thessaly, Greece. Photos by Christian Klein.

truncate apex; spur narrowly cylindrical, (8-)13-20(-22) mm long, straight or only slightly curved downwards, tapering towards acute apex. *Seeds* 0.6-0.8 mm long, cylindrical to ellipsoidal, testa reticulate (Shuka *et al.* 2007).

Etymology: This taxon was originally named as a species, *P. louisii*, in honor of geographer Dr. H. Louis from Berlin, who took part on some of Markgraf's Albanian expeditions (Markgraf 1926; Casper 2004).

Distribution: In contrast to Casper (2004) and Shuka *et al.* (2007), who considered *P. hirtiflora* var. *louisii* (or *P. louisii*, respectively) to be narrowly endemic to central Albania, the author of the present work has studied material from Mount Olympus, Greece, and agrees with Markgraf (1926) that some of these populations also morphologically fall within the range of that taxon. However, *P. hirtiflora* var. *hirtiflora* also occurs on the large Olympus mountain massif (see e.g. Casper *et al.* 2007), but apparently never sympatrically with var. *louisii*, like this is also the case in Albania. Peruzzi (2007) additionally reported and pictured the variety from N Pindhos, Greece (under the name "*P. hirtiflora*"). The range of *P. hirtiflora* var. *louisii* is fully included within the Balkan range of *P. hirtiflora* var. *hirtiflora* (Fig. 1).

Habitat: In wet calcareous meadows or on steep seeping slopes in Albania (Markgraf 1926; Casper 2004; Shuka *et al.* 2007), on limestone rocks near springs on Mt. Olympus, Greece (Ch. Klein, pers. comms.; Fig. 6). At lower altitudes of 150-700(-900) m in Albania (Shuka *et al.* 2007), at ca. 1000-1500 m on Mt. Olympus.

Conservation status: Considered endangered in Albania, as only three populations are known, all in close proximity to cities, and one known site apparently is extinct now due to human water constructions (Shuka *et al.* 2007, in their footnote 34). The known populations at Mt. Olympus, Greece, lie within the borders of a National Park.

Notes: Pinguicula hirtiflora var. *louisii* has sometimes been treated as distinct species, *P. louisii* (Markgraf 1926; Casper 2004). Although it differs morphologically from *P. hirtiflora* var. *hirtiflora* regarding corolla shape (maybe as much as *P. crystallina* differs from *P. hirtiflora*), this certainly is the taxonomically most tenuous member of the complex, as there is full geographical and some morphological overlap with *P. hirtiflora* var. *hirtiflora*; however, this taxon seems to be separated at least cytologically (being a tetraploid) in most populations. Also, the flowers of *P. hirtiflora* var. *louisii*, with entire rounded margins of the corolla lobes and a comparatively long, acute spur (Fig. 7) will generally help to distinguish it from *P. hirtiflora* var. *hirtiflora*. Hence the opinion of Ernst (1961), Casper (1962, 1966), and Shuka *et al.* (2007) is followed here to treat this taxon as a separate

Figure 7: *Pinguicula hirtiflora* var. *louisii* in cultivation. Top: plants from Linza, Albania. Note the comparatively long spur of this variety, as well as the narrow corolla lobes with rounded entire margins. Bottom: Exact locality unknown, "former Yugoslavia", plants from BG Munich (most likely from a location in Albania).

variety. Even the species' original author, Markgraf, later decided to finally follow the recombination of Ernst (1961), and regarded his *P. louisii* as a variety of *P. hirtiflora* (Shuka *et al.* 2007).

Pinguicula hirtiflora Ten. var. *hirtiflora*

Synonyms: *P. crystallina* subsp. *hirtiflora* (Ten.) Strid, *P. hirtiflora* var. *euboea* Beauverd & Topali, *P. hirtiflora* f. *pallida* Casper, *P. albanica* Griseb., *P. laeta* Pant., *P. lavalvae* Innangi & Izzo (in press), *P. vulgaris* var. *hirtiflora* (Ten.) Ces., Pass. & Gibelli

Leaves (20-)30-60 mm long, (5-)15-25(-40) mm wide, broadly elliptical to obovate, with enrolled margins and obtuse to emarginate apex; "winter leaves" slightly to much shorter; leaves yellowish green or tinged purple-reddish, especially near the base. *Scapes* (35-)60-120 mm long, densely glandular. *Calyx* bilabiate, upper lip trilobate (sepals free to the base or fused in the lowermost part), lower lip bilobate, lobes fused for half or more of their length and with their apices obtuse to acute. *Corolla* (13-)16-25(-32) mm long (including spur), bilabiate, upper and lower lip usually spreading at ca. 180° (forming one line), corolla white, usually each corolla lobe with violet-blue tip (but sometimes lobes entirely white), corolla throat and spur yellowish-green, throat sometimes with few reddish-brown stripes; upper two-lobed, lobes divergent, obtuse with emarginate to truncate apex; lower lip deeply trilobed, lobes spreading or slightly overlapping, each with emarginate to truncate apex; spur narrowly cylindrical, (5-)7-13 mm long, straight or slightly

curved downwards. *Seeds* 0.5-0.9 mm long, cylindrical to ellipsoidal, rarely crescent-like, testa reticulate (Shuka *et al.* 2007).

Chromosome number: $2n = 28$ (Mikeladse 1996, Mikeladse & Casper 1997, and Casper & Stimper 2004, 2006 for material from Calabria, Italy; Casper & Stimper 2006 for material from Campania, Italy; Casper & Stimper 2006 and Shuka *et al.* 2007 for material from Albania; Casper *et al.* 2007 and Casper & Stimper 2009 additionally for material from Greece). The repeatedly published karyotypes of $2n = 27$ for this species (for Greece: Strid & Franzén 1981; for Italy: Peruzzi 2004; Peruzzi *et al.* 2007) or ploidy rows ($2n = 16, 24, 32, 48$ for material from Greece: Contandriopoulos & Quezel 1974; Casper 1962) have previously been explained by aneuploidy, but are believed to result from counting errors by Casper & Stimper (2004, 2006, 2009), Casper *et al.* (2007), and Shuka *et al.* (2007).

Distribution: Native to southern Italy (regions Campania and Calabria), the Balkans (Albania, Macedonia), and Greece (regions West Macedonia, Epirus, Thessaly, Central Greece, Peloponnese; Boissier 1875; Casper 1962, 1966; Strid 1991), obviously with an additional outlying finding from Thrakia (Philippos near Drama, Falakro Mountain; sensu Contandriopoulos & Quezel 1974), however which needs confirmation (Strid 1991; no herbarium vouchers of Contandriopoulos or Quezel could be found for this record yet by the author of this article, despite an intensive search); the species is fully absent from the isle of Crete, despite an erroneous mention for that island by Innangi & Izzo, in press). A recent finding of *P. hirtiflora* on Mt. Taygetos, Peloponnese, Greece (http://www.greekmountainflora.info/Taygetos/Taygetos9.html) constitutes its southernmost known occurrence (Fig. 1). This species has been naturalized in NW Italy/SE France (two known populations in the Roya Valley; A. Roccia pers. comms.; Fig. 1), Switzerland (one population at Interlaken, canton of Bern, not shown in Fig. 1) and the Czech Republic (one population in the Beskydy Mountains, northern Moravia; Pyšek *et al.* 2012; not shown in Fig. 1).

Habitat: From sea level (e.g. near Vietri Sul Mare, Campania, Italy, where the plants grow on limestone cliffs reached by the spray during heavy sea) to at least 1700 m altitude in Greece (Steiger 1998). High altitude populations of this species hibernate as open, carnivorous leaf rosettes covered by snow and ice. Growing in permanently wet habitats but in a variety of different soils, such as dripping limestone cliffs (Fig. 8), calcareous seepages, margins of streams, wet serpentine rock, peat bogs and even in live *Sphagnum*.

Conservation status: In Italy, there are a few known populations in Campania (Casper 1962, 1970; Pinto *et al.* 2000; Peruzzi *et al.* 2004; Innangi & Izzo, in press), however these are very localized and rare, and thus the species is considered vulnerable in this region (Peruzzi *et al.* 2004). Only a single location is known from Calabria, which is considered critically endangered, as it is under threat by road construction (Peruzzi *et al.* 2004). In the Balkans *P. hirtiflora* var. *hirtiflora* is widespread and common, although sometimes threatened by road constructions (Shuka *et al.* 2007), in Greece several populations also under potential threat by human activities (Steiger 1998).

Notes: The recently proposed *P. lavalvae* (named after Prof. La Valva of Italy; Innangi & Izzo, in press) represents a pale to white flowered population of *P. hirtiflora*. The variation in shape and size of calyx and corolla lobes, as well as the paler color pattern, fall well in the natural range of *P. hirtiflora* var. *hirtiflora*, as it is known between and within populations in the center of the species' distribution in the Balkans and northern Greece. Such pale-flowered plants have been described earlier as *P. hirtiflora* f. *pallida* from Greece and Albania (Casper 1962, 1966). Due to its wide distribution range, *P. hirtiflora* var. *hirtiflora* shows a remarkable variation in coloration, size and shape of its flowers between different populations (Fig. 9), while the plants remain relatively uniform within a population (Steiger 1998).


Figure 8: Left: *Pinguicula hirtiflora* var. *hirtiflora* as a lithophyte on tufa rocks, Poros, Western Makedonia, Greece. Photo by Thassilo Franke. Right: *Pinguicula hirtiflora* var. *hirtiflora* growing on a limestone seepage wall in the Roya valley, France-Italy border, where the species most likely had been introduced to this site.

Cultivation

Cultivation of members of the *P. crystallina*-complex has often been reported to be notoriously difficult (e.g. Adamec & Pasek 2000). In vitro cultivation of most members of this group has proven difficult to impossible (pers. obs.; K. Pasek pers. comms.; P. Harbarth pers. comms.; S. Ippenberger pers. comms.). However, seed propagation in the greenhouse, outdoors or under artificial lights is no problem. If fresh seed is sown, it will readily germinate, and seedlings can be raised to flowering plants within about 1-2 years. Seed or division of old plants is also the only way to propagate these butterworts, as none of the four species will grow from leaf cuttings from my experience (although Slack 1979 reports having made successful leaf cuttings from *P. hirtiflora*; something which I never achieved in any of the different location forms I grow). But some location forms of *P. hirtiflora* var. *hirtiflora* and *P. crystallina* casually will form adventitious plantlets on short lateral outgrowths from the base of the mother plant (very short lateral stolons, not exceeding the overall rosette diameter, so that the adventitious plantlets will usually emerge densely packed to the mother rosette). Further, the rosettes of old healthy specimens of all four species will also regularly divide from the center, usually in spring when in full active growth (but more rarely and to a much lesser degree in *P. hirtiflora* var. *louisii*). So the pots will slowly crowd with several rosettes, even if you started with just a single plant.

My personal experience is that these four species dislike any root disturbance, as most problems and losses arise after repotting. Therefore, the plants are best sown directly into large pots, where they can remain for a long time without removal. Adrian Slack, in his outstanding book on carnivorous plant cultivation, wrote about *P. hirtiflora*: "[...] An easy and worthwhile plant.", but he also correctly pointed out a crucial point for its cultivation, when stating that "[a]ll the *Pinguicula* hate root disturbance, and should never be repotted while in summer growth. This will almost certainly result in the death of many[...]" (Slack 1979). While I, personally, cannot confirm this for "all the *Pinguicula*" species I grow, this indeed seems to be particularly true for the homophyllous species not forming winter buds (including the *P. crystallina*-complex).

A variety of soil mixes have been used successfully for these species by different growers – my experience is that more clayey substrates will work better than pure peat-sand mixes. I have been using a mix of three parts *Sphagnum* peat, one part grey clay and one part quartzitic sand (for *P.*

Figure 9: The flowers of *P. hirtiflora* var. *hirtiflora* are quite variable in corolla size, shape and coloration. Top: Plants from Aqua Santa, Napoli, Campania, Italy (type locality); Center: from Rossano, Calabria, Italy; Bottom: from Vietri Sul Mare, Campania, Italy.

crystallina from serpentine locations and *P. megaspilaea*) with the addition of another part of calcareous sand or tufa gravel for those growing in alkaline soils (*P. hirtiflora* var. *hirtiflora*, *P. hirtiflora* var. *louisii*, and *P. crystallina* from limestone locations). But all species of this affinity neither seem to be strict calcifuges or calciphiles, and as several *Pinguicula* enthusiasts have told me, all species will happily grow in more or less the very same soil mix.

Cool growing conditions are favoured, and all four taxa grow well for the author in a cool greenhouse, in an area that is shaded from hot summer sun by the aid of shade cloth. Montane location forms of *P. crystallina* and *P. hirtiflora* var. *hirtiflora* will also do well outdoors year round in an

Figure 9 (cont.): Top: from Këlcyra, Albania; Center: from Librazhd, Albania; Bottom: from Mount Olympus, Greece.

alkaline bog garden, in trays or pots, providing protection from bare frost and winter sun (in areas with regular snow cover, growing these species outdoors will cause no problems, otherwise some artificial winter protection by brushwood or cloth is recommended).

Finally, I want to strongly discourage introducing any of these species to natural sites (whether outside or within their natural growing range), as their seed set and vegetative propagation can be enormous in suitable habitats, hence they can constitute a potential invasive threat to native flora. This happened for example in the Roya Valley, along the border of NW Italy and SE France, where naturalized *P. hirtiflora* var. *hirtiflora* of unknown origin has shown to be very invasive, now growing as dense mats on dripping rocks, that suppress the naturally occurring *P. reichenbachiana* at

the same site (A. Roccia pers. comms.; Fig. 8). *Pinguicula hirtiflora* var. *hirtiflora* also has been naturalized at a site in the Czech Republic, where this species had been deliberately planted on a tufa cascade and since forms a spreading population (Pyšek *et al.* 2012).

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